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A NEW FOSSIL PLANT FROM THE NEW ALBANY SHALE WITH SOME COMMENTS ON THE ORIGIN OF LAND VASCULAR PLANTS*

PART 1. CROCALOPHYTON, A NEW TRANSITIONAL SEA-LAND PLANT

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Introduction:—

The Devonian-Mississippian black shales of the east-central states have yielded in recent years a fossil flora that is remarkable in the unique and diversified nature of the plants. Within this broader area the New Albany shale of Kentucky and Indiana has produced an exceptional wealth of plant fossils. It is noteworthy that so great a variety of plant groups has been described since the collections from this area and horizon are not abundant. Few, if any, of the plants composing the flora are known with a completeness that is in any way satisfactory, yet in spite of the fragmentary nature of the specimens, they reveal plants that are novel in their morphology and anatomy and disclose major taxonomic groups hitherto unknown. The additional fact that several competent paleobotanists have not found it possible to agree on the affinities of certain constituents of the flora is indicative of its exotic nature.

It is the purpose of the present paper to record a distinctive and particularly problematical new member of the flora from a locality in Kentucky. In view of its perplexing taxonomic status a discussion follows (Part 2) dealing generally with some of the problems of the evolution of land plants which seem to be inextricably related to the particular problem of our fossil's affinity.

The geology of the New Albany shale has been dealt with in the comprehensive study by Campbell (1946) and the fossil plants of the area with which we are concerned have been described by Read and Campbell and by Hoskins and Cross. It seems unnecessary to review these previous paleobotanical studies although we

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have included in the "Literature Cited" section a fairly complete list of the contributions on the subject.

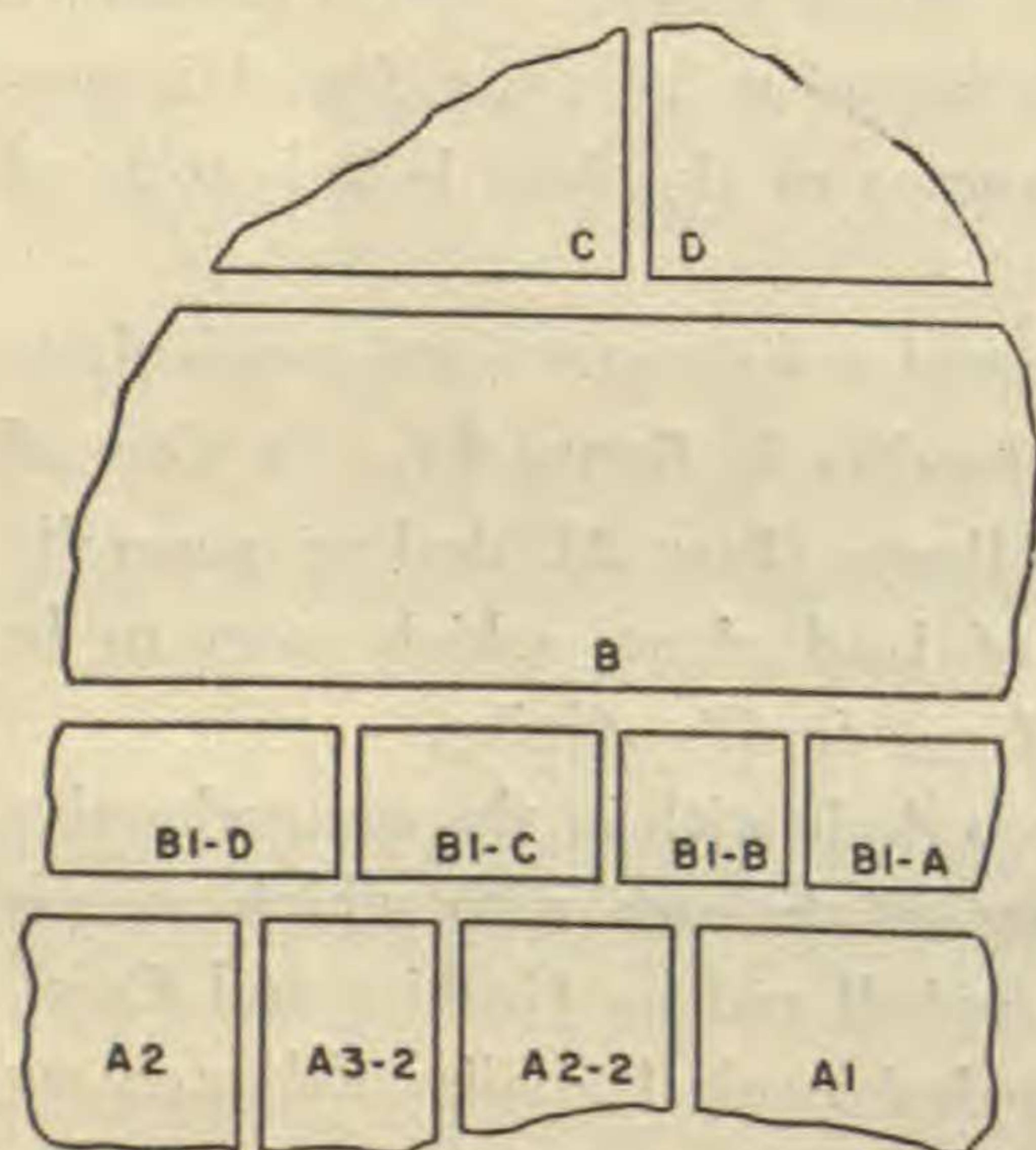
The reader will perhaps agree, if from only a casual glance at the illustrations, that a few additional words of introduction may be justified. Our study of this fossil has proven to be a fascinating if somewhat precarious venture; fascinating in that it is anatomically the most unique fossil that has ever come into this laboratory, and precarious in that its affinities remain, at the conclusion of our studies, quite uncertain. Suggestions are offered on later pages concerning its possible position in the plant kingdom, but, quite admittedly, these are speculative although we hope that these speculations may prove to be of some significance.

It was evident from an initial inspection of the fossils that the cellular organization was highly unique, so much so in fact that consideration was given to the possibility that it was of animal origin. However, detailed studies of the cellular structure have left no doubt as to its plant nature, and other botanists who have been kind enough to examine our preparations have agreed on this point.

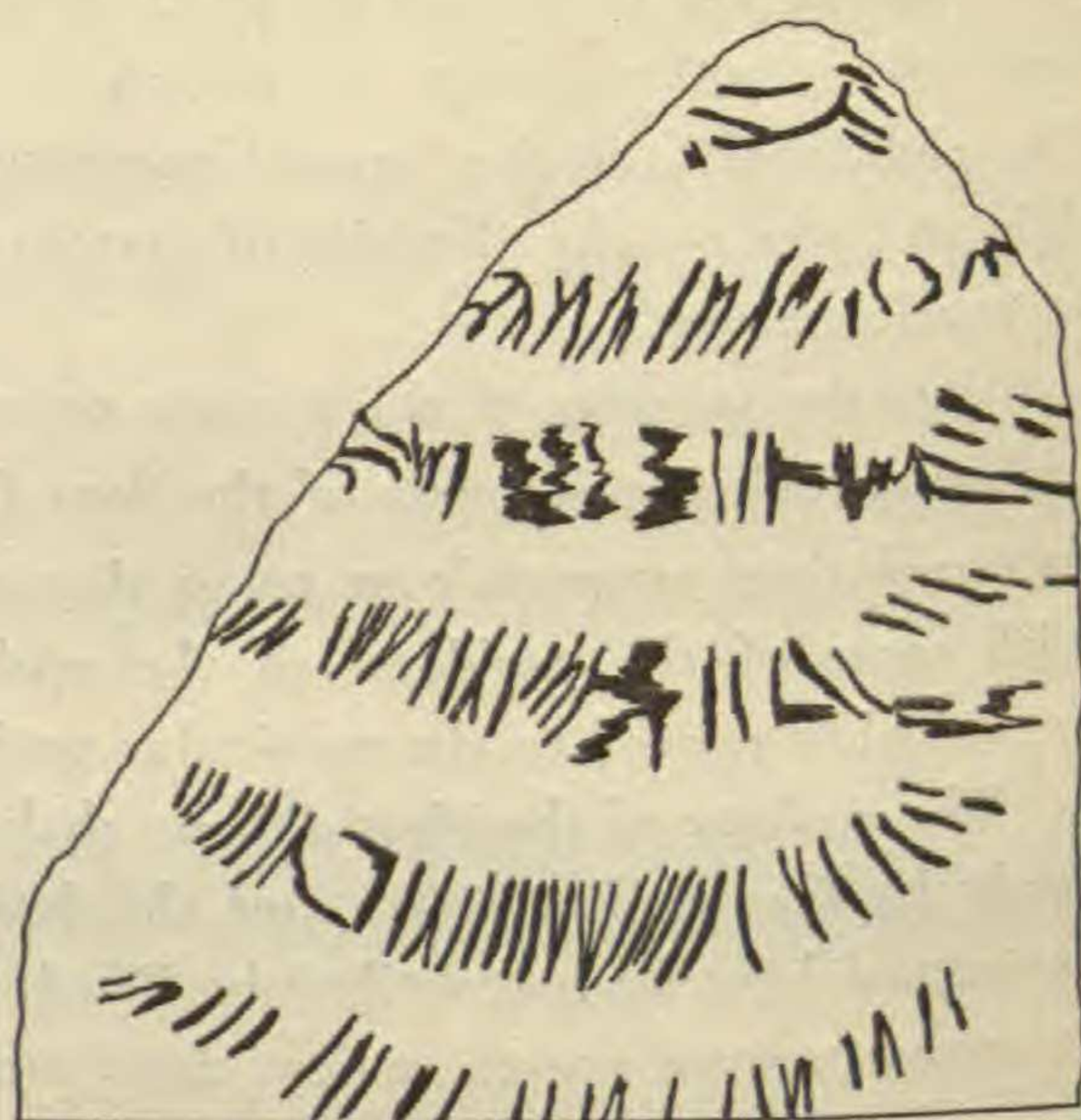
Description:—

The following description is based on two specimens that were collected several years ago by Mr. Charles B. Read (U. S. Geological Survey) from the New Albany shale at a locality near Boston, Kentucky. We are indebted to Dr. S. H. Mamay, who is in charge of the Geological Survey's Paleozoic plant collections, for kindly placing the two specimens in our hands for study. The specimens and all figured slides are now preserved in the collections of the U. S. National Museum.

Since the two specimens are very nearly identical in size and form and the surfaces revealed, under low magnification, apparently identical anatomical



Text-fig. 1. Longitudinal profile through specimen U.S.N.M. No. 40797, showing surfaces from which thin sections were prepared.



Text-fig. 2. Longitudinal section through the major axis showing the stratified organization of the fossil. Strands are shown in black.

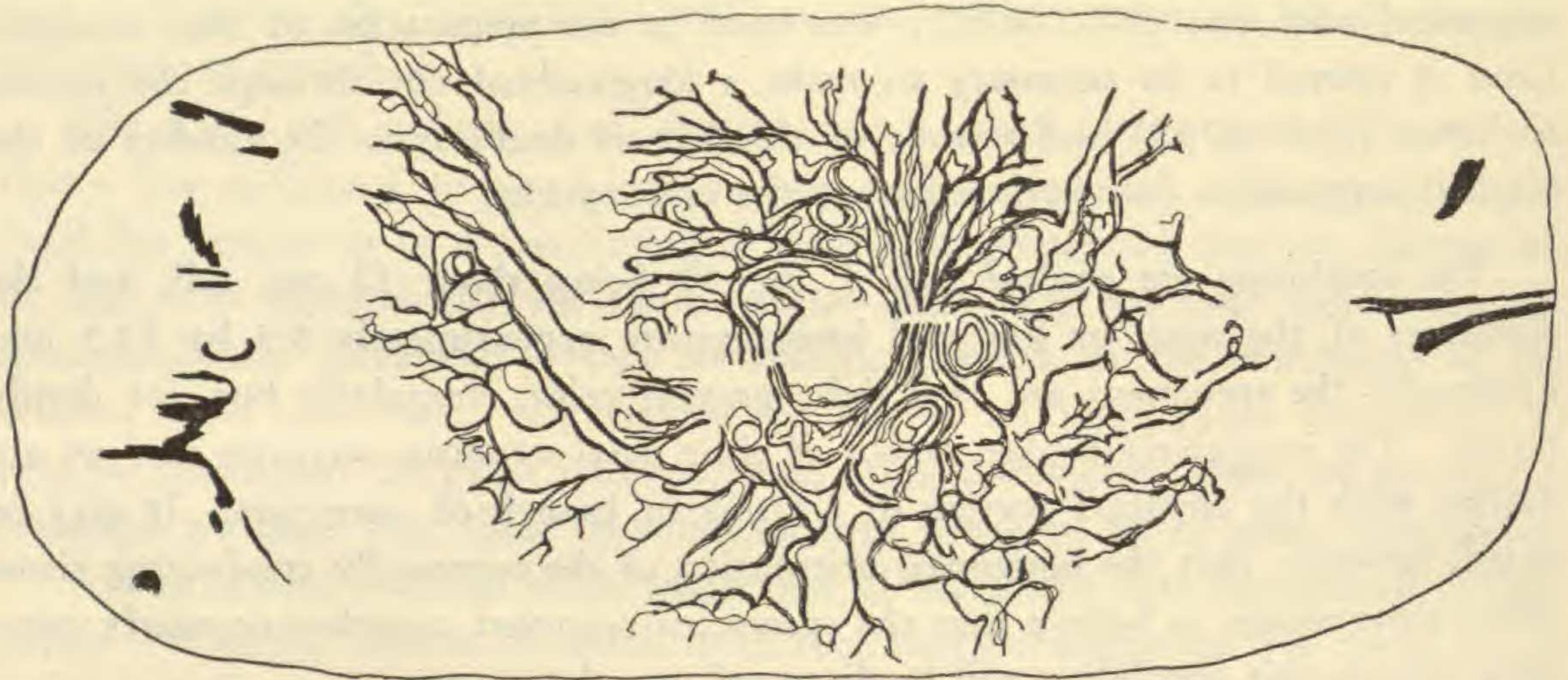
structure, only one (No. 40797) was used in the preparation of thin sections. Later it proved to be necessary to make a longitudinal cut through the second specimen (No. 40798) and a study of this left no doubt as to the validity of the original supposition that both represent the same species.

The specimens are conical (pl. 4, fig. 1) being about 12 cm. tall, and the diameters of the more or less oval base measure approximately 5.5 by 11.5 cm. Externally the specimens are of a light grayish color, irregularly but not deeply pitted. The irregularly broken aspect of their basal structure suggests that we are dealing with the terminal portion of a trunk or branch of some sort. It may be noted, however, that the horizontal orientation of the supposedly conducting tissue offers some reason to believe that the specimens represent complete or nearly complete plants; this possibility will be discussed on a later page.

Text-fig. 1 presents in profile the plan that was followed in studying specimen No. 40797. Numerous transverse and longitudinal sections were prepared from the A, B, C and D blocks, sufficient to insure a representative coverage of the internal structure.

Although the preservation of the specimens is excellent the original plant material has been highly replaced by phosphate of the calcium-magnesium group. This lack of a sufficient mineral-organic differential, combined with the fact that the specimens are rather soft and porous, prevented the use of the peel technique. No difficulty was encountered, however, in preparing ground thin sections. The blocks to be sectioned were allowed to stand in melted resin for a few minutes before affixing to the slide. The only particular caution found to be necessary was very careful grinding in the last stages due to the softness of the petrification.

The general organization of the fossil, which has been given the new generic name *Crocalophyton* is shown diagrammatically in text-figs. 2 and 3. The specimens are composed of but two tissues, one consisting of ray-like strands made up of transversely elongated cells, the strands being enclosed in a thick-walled, nearly isodiametric parenchyma. Whether the term parenchyma is appropriate may be questioned; it is at least as fitting as any that we are aware of. The strands are shown in black in both figures. Text-fig. 3 is taken from the lower surface of the B1 block. The figure was prepared from four transverse sections taken from B1A, B1B, B1C and B1D as shown in text-fig. 1. After each section was photographed, the strands were inked; the four photos were then pasted together and a tracing prepared of the entire cross-section. Text-fig. 2 is a diagram of the arrangement of the same tissue system in a median longitudinal surface; this was prepared from a free-hand sketch of the surface as it appeared under a binocular microscope. It may be noted that these figures are intended to show the approximate organization of the larger strands and that the photos should be relied upon for a precise portrayal of their structure and pattern of organization.



Text-fig. 3. General organization of the strands in transverse section prepared from the basal surface of the B 1 block.

The Strands:—

The term *strand* is applied to the highly unique ray-like tissue system of the fossil. The cells composing the strands are transversely elongate and pitted; they are presumed to have functioned as a radially conducting system and are tentatively thought to be a primitive tracheidal or sub-tracheidal cell type.

In their organization the strands, as shown in text-fig. 3, tend to radiate from the central part of the specimen toward the periphery; this is, however, only a very general tendency. It will help to clarify the nature of this curious tissue if we glance next at fig. 3, which is a photograph of a representative portion of the cross-section. It shows an area of approximately 1.0×1.5 cm. considerably enlarged. A comparison of this with text-fig. 3 reveals the fact that the latter does not include the numerous smaller strands that occur in many parts of the specimen.

There are few strand terminations in the central part of the fossil although occasionally the smaller ones end blindly. They form for the most part a continuous and highly complex anastomosing system; a few continue to the extreme periphery of the fossil and some end abruptly within a few millimeters of the periphery.

The strands vary from one to nine cells wide and are vertically elongate sheet or ray-like structures. One must, as in the case of wood rays, observe tangential and radial sections in order to acquire an understanding of their 3-dimensional structure. While they present a superficial similarity to the wood rays of a conifer or dicotyledon it is evident from text-fig. 3 and fig. 3 that they are by no means comparably oriented.

Referring to fig. 3 (pl. 4) it will be noted that two lines have been drawn in the lower right portion of the photo. When a longitudinal section is prepared in the "A-A" plane (referred to as *tangential*) the rays appear as shown in fig. 4 (an

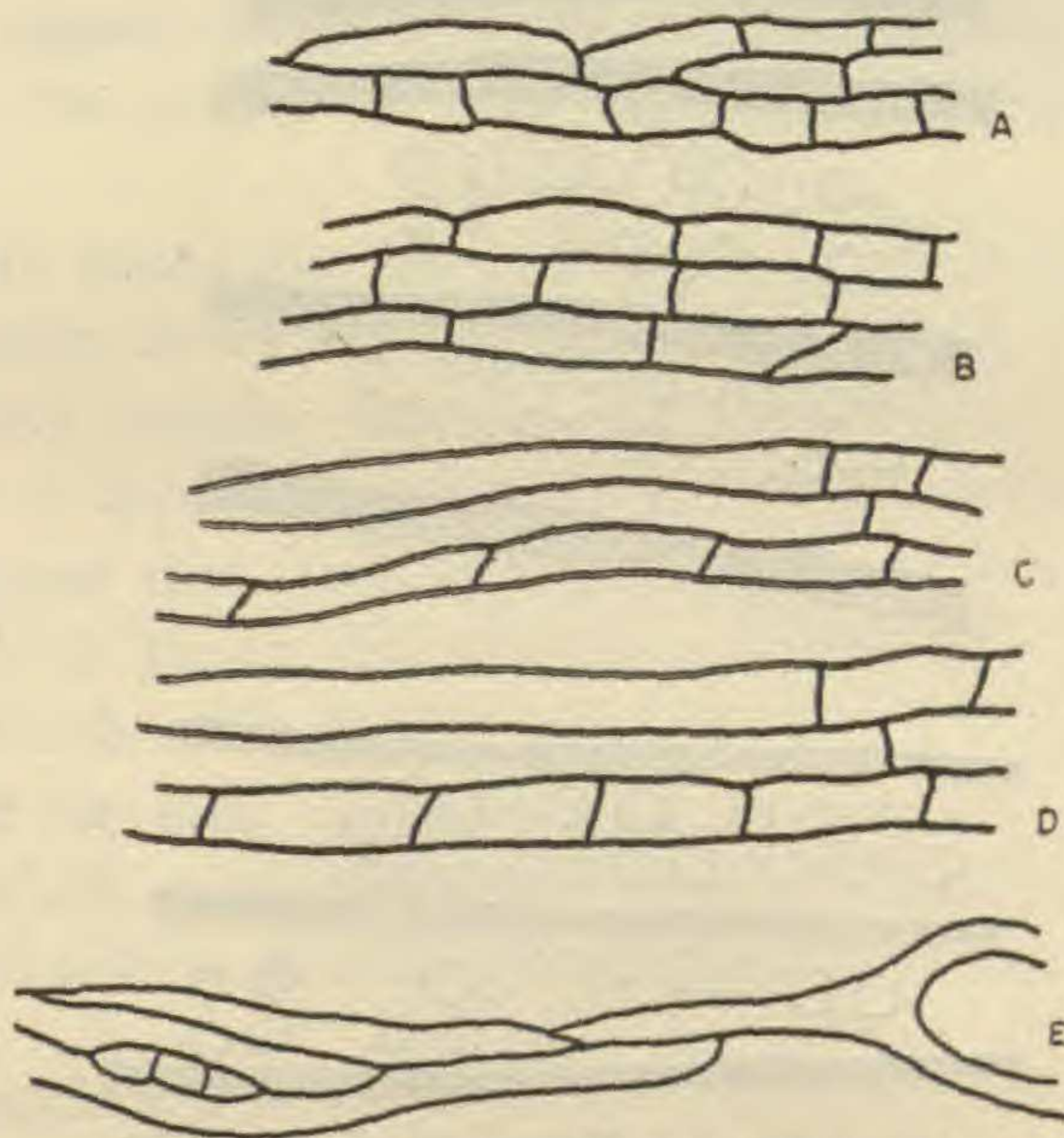
appreciably higher magnification than fig. 3); and longitudinal sections prepared in the "B-B" plane (referred to as *radial*) reveal the rays as shown in fig. 5.

The strands are about 1 cm. high and, as shown in the longitudinal profile (text-fig. 2), they are distinctly stratified. Thus a transverse section taken between the strand areas will reveal no strands. Most of them terminate blindly although a few continue to the periphery of the specimen (text-fig. 3). The tortuous pattern of the strands is emphasized in fig. 2 (and parts of fig. 3) where they present a circular pattern in transverse view.

There is no externally delimiting tissue. The only evidence which suggests that the original surface of the fossil is intact is the close similarity of the two specimens. It is of course possible that some outer tissue or tissues was lost prior to fossilization.

Detailed Structure of the Strands:—

Any transverse section (figs. 3, 6, 7) clearly reveals the variation in the width of the strands which may take place within a few millimeters due to the anastomosing pattern of this tissue and to the frequent intercalation of parenchyma cells.

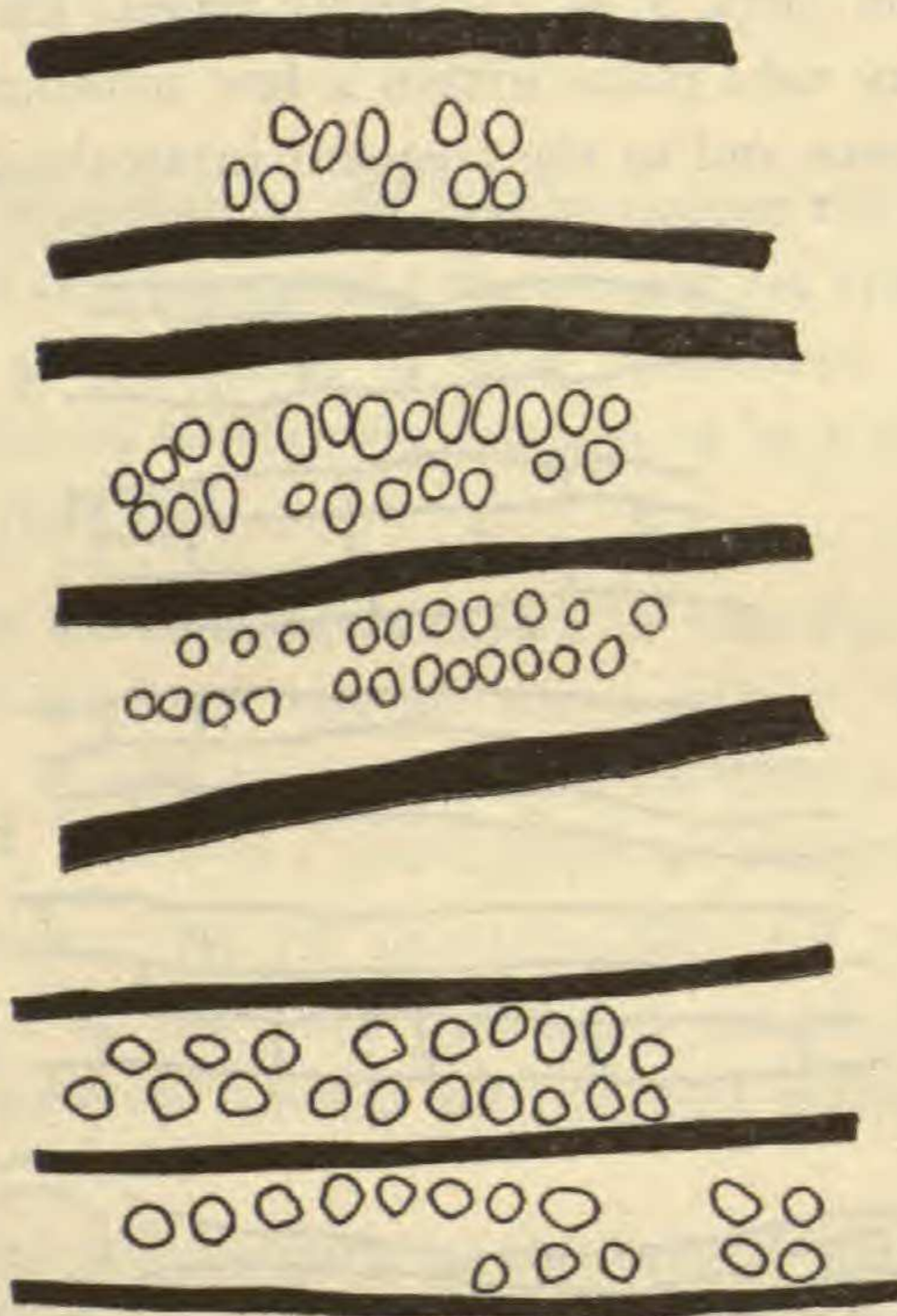


Text-fig. 4. Representative portions from several strands showing shape of strand cells.

One of the most striking characteristics of the strands is the organization of the cells in very nearly perfect vertical rows; this is clearly shown in tangential sections (fig. 4). The cells are transversely elongate, their length appearing to be extremely variable. In tangential view the strand cells are approximately square, being 38μ in diameter, while their length, as observed in cross-section (figs. 6, 7), varies between 105 and 230μ . Some cells, however, have been followed for a considerably greater distance without any evidence of terminations, but where they have been observed they are for the most part transverse. Representative portions of strands are shown in text-fig. 4 where figures A, B and E were drawn

from strands in transverse section and figures C and D from radial sections. While some of the cells possess a tapering end, transverse or only slightly oblique end walls are more usual.

The pitting in the strand cells is particularly interesting. In our initial suite of slides many of the cells displayed obscure striations that were suggestive of some sort of wall sculpturing but it was not until several radial sections were examined with considerable care that clearly defined pits were found. Knowing then what to look for they were found in several slides and we are reasonably confident that the pitting is uniform on both the transverse and radial walls of most or all of the strand cells. In fig. 5a and 5b are shown portions of two particularly well-preserved strand cells in radial view, and the structures which are interpreted as pits appear in two rows wherever they have been observed with clarity. Text-fig. 5 shows pitting in cells from two selected areas. No indication



Text-fig. 5. Pitting in the "radial" walls of the strand cells.

of a border has been noted and the slightly angular outline renders them somewhat distinct from the bordered pits of most vascular plants.

The Parenchyma:—

The only cell type other than the strand cells is the tissue enclosing the strand cells which has been referred to as parenchyma. This consists of cells which are variable only within rather narrow limits and are for the most part isodiametric; rarely are these cells more than twice as long as broad. A representative portion of the parenchyma is shown in fig. 10. The transverse diameter of the parenchyma cells (fig. 10), based on measurements of 140 cells, was found to vary between

45 and 122 μ , with an average of 80 μ ; in longitudinal view (fig. 9) their length, based on measurements of 70 cells, varies from 52 to 165 μ , with an average of 100 μ .

The above figures are based on what is termed, as a matter of convenience, "ordinary" parenchyma, referring to the relatively large areas where the parenchyma is not associated intimately with the strands (fig. 3) or with the purely parenchymatous "inter-strand" portions of the specimen (text-fig. 2). The parenchyma between closely associated strands consists of cells that are slightly elongated vertically and arranged in regular rows, assuming an organization comparable with that of the strand cells. Fig. 11 shows a representative portion of such parenchyma between two strands appearing at the extreme left and right edges of the photo. Parenchyma cells in such areas also may show a tendency to be elongated transversely; this is evident between some of the strands illustrated in fig. 3.

Aside from these structural variations, which certainly are not extreme when compared with the generally bizarre characteristics of the fossil, there is no evidence to suggest any appreciable differences in the functional nature of the tissue.

The walls of the parenchyma cells are rather thick, being approximately 6-7 μ . This character may appear exaggerated due to the difficulty of distinguishing, in the photos, between the actual cell wall and the mineral layer in the periphery of the lumen.

Although we have stated that the parenchyma and strands constitute the only two cell types, one other structure may possibly be distinct. It may be noted that all of the photos which include any appreciable quantity of the fossil (figs. 3, 4, 8) display open areas or apparent breaks. In a very few instances we have observed structures which suggest that some sort of secretory areas may be present. It is apparent, for example in fig. 12, that the central cells are in an advanced stage of disintegration but whether this cavity is a secretory structure or simply decay cannot be determined for sure. In only two or three cases we have observed that the parenchyma cells are radially aligned (fig. 13) in such areas. These are so few that it is problematical as to whether any significance can be attached to them.

The Ontogeny of Crocalophyton:—

The arrangement of the strand cells and closely associated parenchyma in very nearly perfect vertical rows (figs. 4, 11) seems to imply meristematic activity of some sort. Judging from the characteristic alignment of these cells they were formed by an apical meristem which laid down, successively, the strand and inter-strand layers or, at an early stage in the plant's development, several meristematic areas were differentiated. Whether the strands may be termed "xylary" is certainly debatable. The cells are perhaps best termed "pre-tracheidal"; they are elongate and pitted and probably served as conducting elements but the organization and orientation of the strands can only be said to be unique.

If the argument presented in Part 2 is in any way valid the organization of the fossil is not as surprising as may at first appear. Meristematic activities are perhaps

more varied in plants than is generally realized, and it is more than likely that the algae, from which we suppose land vascular plants arose, experimented rather widely in this way and in some cases succeeded.

Without necessarily implying a brown algal ancestry for any of the dominant pteridophytic groups of the Devonian it is difficult to study living representatives, such as *Pterygophora* with its stipe of radially aligned cells, "annual rings," and its trumpet cells (Smith, 1939), without visualizing tendencies that were used to advantage in the creation of a land flora.

With reference to the habit of land vascular plants it is evident that xylary systems evolved along many different lines. Of particular interest here is *Schizopodium davidi* (Harris, 1929) from the Devonian of Australia. It is described as having an outer wood zone "intermediate between primary and secondary wood", the tracheids being cubical, vertically elongate, radially elongate or tangentially elongate, and apparently not formed by a clearly defined cambial meristem. This "outer xylem" may be considered a fumbling attempt (probably one of many) of the plant to produce secondary wood. *Crocalophyton* may be looked upon as a plant in which a unique, and apparently unsuccessful, mode of meristematic activity made its appearance. It is perhaps most aptly summarized in the words of one botanist who examined our illustrations, as a "kind of foolish experiment" that was involved in the evolution of land plants.

*Crocalophyton readi*¹ gen. et sp. nov.

Diagnosis of the Genus and Type Species: Conical-shaped structure, about 12 cm. tall with a roughly oval base measuring approximately 5.5×11.5 cm.; stratified in a plane perpendicular to the long axis and consisting of strand-parenchyma bands alternating with parenchyma bands; strands about 1 cm. high, generally radiating from the center but forming a highly irregular system frequently branching and anastomosing and contorted to the extent of forming a loop, or series of loops, 1-9 cells wide (transverse), with the cells arranged in vertical rows; strand cells horizontally elongated with mostly transverse end walls and two rows of apparently simple pits in the longitudinal walls.

Type specimen: United States National Museum, No. 40797.

Locality: near Boston, Kentucky.

Horizon: New Albany shale; Upper Devonian or lowermost Mississippian.

Affinities: On the basis of our own observations and the opinions of specialists familiar with the various cryptogamic groups, *Crocalophyton* shows no evident relationship to any known thallophyte, bryophyte or pteridophyte. Since its affin-

¹ On the assumption that this was a plant that lived in a habitat transitional between strictly aquatic or dry land, the first syllable of the generic name is taken from the Greek *krokale*, meaning beach or seashore; the specific name is in recognition of Charles B. Read's studies of the New Albany shale plants.

ities are so very vague we have felt that nothing is to be gained at the moment by setting up any new taxon such as a family or order. A more detailed consideration of the possible relationships of the fossil is included in Part 2.

PART 2. SOME COMMENTS ON THE ORIGIN OF LAND VASCULAR PLANTS
AND THE TAXONOMIC POSITION OF CROCALOPHYTON

HENRY N. ANDREWS

In his introduction to a consideration of the problems of Jurassic paleobotany Harris (1947) made the following comment:

Most of the "problems" of paleobotany are those questions which we feel we would like to be able to answer but cannot because our knowledge is incomplete. Such problems are often ephemeral. In time some are answered; some are left aside by progress because they cease to be interesting, or are later realized to be meaningless;

I would supplement this with a paleobotanical proverb that has been attributed to D. H. Scott, although most paleobotanists must have felt at one time or another, that: "fossil plants frequently create more problems than they solve". This is not intended as a facetious comment; it points to the great complexity and diversity of organization that existed in many groups and we are forcefully reminded on occasion of the necessity of altering our concepts of the lines of racial origin and development within a group.

The problem of the origin of vascular plants has been with us for a long time; it is not one of the ephemeral ones and if it is solved, at least in part, it will have proved to have been a multi-faceted problem involving development along several (or many) morphological lines. Many of us have become accustomed to look upon *Rhynia* as *the* primitive land plant; there is now concrete evidence to suggest that it is *a* primitive vascular plant representing a particular line of pteridophytic evolution. In the following pages I should like to discuss what seems to me to be the nature of the problem; this is essentially a review although it may possibly assist in clarifying the issues that are involved. The discussion is also aimed specifically at the question as to just why *Crocalophyton* does not conform to any taxonomic category in the plant kingdom.

The structure of *Crocalophyton* is quite unlike that of any known alga. The possibility that it might be a member of the Phaeophyta was considered, but the organization of the strands could be correlated in no way with the anatomy of any brown alga. Several competent algologists have examined the illustrations and have readily agreed that the plant has no place in the algae. As to the vascular cryptogams there is equally little to choose from. *Crocalophyton* is unique in the ray-like organization of the strands with their radially elongated, pitted cells arranged in vertical rows. The pits show no evidence of a border, and the shape of the cells is not closely comparable with that of a tracheid.

Thus, lacking any clues that might suggest affinities with a known group of plants it can be considered only on its own merits.

On the supposition that the strands constitute a conducting tissue of sorts a guess may be made as to the plant's mode of life. The stratification of the strands, being separated by rather broad bands of distinctly non-conducting tissue (the parenchyma), combined with the radial elongation of the strand cells, would seem to imply that whatever transport capacity the strands served was primarily transverse rather than longitudinal. It is also unlikely that such a plant could have attained any great height if it existed in a strict land habitat. If we next assume that it lived submerged at a depth of as much as several fathoms, as do some of the Phaeophyta, the trunk might have attained a considerable length but in such a habitat it is difficult to understand why so profusely developed a conducting system was needed. Since plants do seemingly strange things that do not always conform with our understanding of their "needs", this possibility need not be entirely ruled out.

If we postulate next an intermediate habitat, approximately in the tidal zone,² a possible case for the strands may be made. A relatively short but stout trunk attached to the rocks between low and high tide marks, and perhaps even somewhat beyond the latter, lacking a root system or any other specialized organ of water intake, would necessarily have to depend upon the absorption of water by the surface of the trunk. Assuming a fairly strong absorption capacity for the exterior surface the strand system could have readily conducted the water throughout the trunk.

The assumption that *Crocalophyton* is a primitive semi-land plant, yet can be assigned to no living or fossil group, would seem to call for further explanation. Two general problems may have some real bearing on the subject. The first is the gap that exists between the earliest land vascular plants and the algae from which they are presumed to have evolved. The second, and I believe correlative, problem is the evolutionary pattern that exists in any major group of plants. Briefly, the concept that I wish to explore is that any large group (lycopods, articulates, "ferns", psilophytes, etc.) is highly polyphyletic and the transitional members between it and the group(s) above it, if it so evolved, may be expected to be correspondingly varied.

As a starting point, a few comments might be made on the origin of the algae as well as their pre-Paleozoic and early Paleozoic record. The earliest record of structurally preserved thallophytes is that reported by Tyler and Barghoorn (1954) wherein they describe fossils that are tentatively assigned to the blue green algae and "simple fungi" from rocks in southern Ontario that are dated as being in the vicinity of 1300 million years and possibly much older. These authors note that, "Since the pre-Cambrian flora with which we are dealing comes from near the base of the Gunflint formation, it seems likely that age may approach 2 billion years."

² It has been called to my attention that the present discussion implies an origin of land vascular plants from marine algae. I wish to acknowledge this criticism and indicate that the evolution of vascular plants from plants of fresh water habitats or waters of varying salinity is not intentionally precluded.

Another recent contribution suggests an even greater age for the algae. In 1941 Macgregor described supposed algal remains from Rhodesia in rocks which have been dated as "at least 2,600 million years" and possibly in excess of 2,700 million years. Since they are not structurally preserved I feel that a considerable element of doubt surrounds these Rhodesian algae; so far as I am aware, the Tyler and Barghoorn report gives us the oldest authentic date of a structurally preserved plant on the earth.

Before returning to the algae, for the purpose of my argument, a few words on the earliest records of vascular plants will be interpolated here. The earliest unquestioned record of such a flora is the mid-Silurian one (*Baragwanathia*, etc.) described by Cookson and Lang from Australia. It is evident that these plants were separated by a broad gulf of evolution from any algal ancestors.

Recently Krishtofovich (1953) has reported a supposed lycopodiaceous plant from the Middle Cambrian of the Aldan Mountain range in Siberia. The plant remains were associated with trilobites (believed to correspond to the *Paradoxides forchhammeri* zone of Western Europe) and according to the author, "Consequently the geological age of the find constitutes no doubt whatever."³

Krishtofovich's *Aldanophyton antiquissimum* is represented by shoots up to 13 mm. wide and 8.5 cm. long which are covered with microphyllous leaves up to 9 mm. in length. "In places a thin rod-conducting bundle may be traced as far as the base of the enations (leaves)". Comparison is drawn with other early lycopods such as *Drepanophycus* and *Baragwanathia* although sporangia were not found in *Aldanophyton*.

There have been several accounts of spores from the Cambrian which are purported to be those of land vascular plants. Several Indian investigators (Jacob et al., 1952, '53a, '53b) have described spores and wood fragments from the Middle and Upper Cambrian of Kashmir, Spiti, and other Indian localities. As many as 43 different spore types are recorded including those referable to Equisetalean plants, "other primitive pteridophytes" and the Pteridospermae. These authors are insistent that their preparations are free of contamination and, although I am prepared to accept the existence of vascular plants in pre-Silurian times, the occurrence of the Pteridospermae in the Cambrian is a matter that will require more substantial proof. Naumova (1949) reports a considerable assemblage of spores from the lower Cambrian blue clay of the Estonia-Latvia-Lithuania area (details of locality are not given) which are presumed to represent bryophytes and pteridophytes.

Since the approximate date at which vascular plants first appeared has some bearing on this discussion the high degree of complexity that already existed in the lowermost Mississippian and Devonian seems significant.

³ Although I have had access to the original publication it is in Russian with no summary in any other language; I am indebted to Dr. Harlan P. Banks, who kindly supplied me with an English translation.

Largely as a result of Florin's important contributions, we are particularly well informed on the evolution of the cordaite-conifer line and certain associated groups. With reference to the origin of this assemblage Florin (1949) notes:

The Ginkgoinae, Cordaitinae, Coniferae and Taxinae undoubtedly belong to the same natural plant group of higher order, . . . but they constitute parallel evolutionary lines which probably were already separated from each other in Upper Devonian or Lower Carboniferous times. At all events, a clear differentiation can be seen as far back as the available fossil records go. [pp. 101-102].

Judging from its stem anatomy the well-known and widely distributed Devonian *Callixylon* is in all probability a coniferophyte and possibly a rather highly specialized member of the group; the fact that it was a large forest tree would suggest that the coniferophytes may date back to an earlier period than the Devonian.

It is also pertinent to note the early appearance of heterosporous ferns, specifically *Archaeopteris latifolia* (Arnold, 1939) from the Upper Devonian (possibly upper Chadakoin) of Pennsylvania, and *Stauropteris burntislandica* (Surange, 1952) from the Lower Carboniferous (Calciferous Sandstone series) of Pettycur, Scotland. Just how these plants fit into the general stream of "fern" evolution is problematical but there can be little doubt that they represent the culmination of a long period of evolution of land vascular plants.

It is perhaps not surprising to find that the angiosperms are not to be excluded from this general retrenchment in time of so many major groups. Under the new binomial *Sanmiguelia lewisi*, Brown (1956) has reported leaves from the Dolores formation (Middle to Late Triassic) of Colorado. They are alternate, large, pleated, monocotyledonous, and closely resemble those of a palm. If this apparent relationship is correct *Sanmiguelia* is the earliest angiosperm on record and suggests a Paleozoic origin for the group.

In view of the evidence, direct and indirect, cited above I do not find it difficult to accept land vascular plants in the Cambrian as a possibility or even a probability.

Next to be considered is the status of the algae during the approximate time when plants were becoming established on the land. A few records based on fairly well-preserved plants indicate the presence of several modern groups of algae in the Devonian. These include smaller algae referable to the Chroococcaceae, Ulotrichaceae and Desmidiaceae from the Onondaga chert of New York (Bashnagel, 1942); Charophyta from the Lower Devonian Downtonian beds (Croft, 1952) of west Podolia (borders of Poland and Russia); fossils referable to the brown and red algae from New York (Fry and Banks, 1955); and the remarkable fungi and algae from the Rhynie chert (Kidston and Lang, 1921). There is abundant evidence that such diversity, comparable with that of today, existed long before the Devonian—Fenton (1946); Fenton and Fenton (1939); Johnson (in Smith, 1951); Pia (in Hirmer, 1927); Walcott (1919), and numerous other references cited by them.

The vast period of time that the algae existed prior to the advent of land plants, even assuming their existence in the Cambrian, is somewhat startling. In a

chart⁴ recently prepared by the U. S. Geological Survey the beginning of Cambrian time dates back 520 million years and the mid-Silurian about 340 million years.

Accepting the mid-Silurian "*Baragwanathia flora*" as the oldest authentic record of vascular plants and subtracting this (340 million years) from the figures of Holmes or Tyler and Barghoorn cited above we find the algae existed from 960 to 1360 million years before the advent of land vascular plants. If we accept Krishtofovich's report of a Siberian lycopod from the Cambrian the figures are decreased by another 100 to 200 million years, but we are still faced with the apparent possibility that the algae existed for one billion years before migration to the land was accomplished.

Unless land vascular plants did evolve much earlier than mid-Silurian times, and by "much earlier" I imply at least several hundred million years, the obvious and baffling question is why was the transition from an aquatic to a land habitat so long delayed? This query is not a new one, and I allude to it only to present two theories that may constitute a fresh approach whether or not they contribute to the solution: *One*, that there existed prior to Silurian (or Cambrian?) times environmental conditions that rendered the transition difficult or impossible. *Two*, that there was a great diversity of plant form involved in the transition and that plants of the *Rhynia* type represent a successful arrival in but one of many different lines that made the try.

As to the environmental factor, I have been intrigued with a suggestion by Rachel Carson in 'The Sea Around Us'.⁵ Assuming a closer proximity of the Moon to the Earth in pre-Paleozoic times she postulates that the action of the tides may have been vastly greater than at present creating a littoral zone, surrounding the oceans, of such turbulence as to render the landward migration impossible. There are obvious difficulties to accepting this as a significant explanation but it is at least thought-provoking.

The second factor mentioned above, namely, the diversity of plant form that may have been involved in the sea-land transition, may have a real bearing on the taxonomic position of *Crocalophyton*.

Evolution in certain major groups, such as the lycopods or articulates, has been a process of extreme polyphyletic once the basic morphology of the group was established. The guess may be hazarded for larger groups, such as the coniferophytes or angiosperms, that they were polyphyletic from the start. The early land plants (excluding clearly defined representatives of the lycopods or articulates) present a highly complex assemblage; some may be justifiably classified as psilophytes while others do not fit with any degree of comfort into any major category and seem to imply a highly polyphyletic origin from the algae.

Few writers of text-books now portray the "family tree" of the plant kingdom

⁴ Prepared from the Report of the National Research Council, Committee on the Measurement of Geologic Time, 1949-50.

⁵ See p. 158 of the original Oxford University Press edition.

as a great central trunk from which secondary branches progressively arise. Such diagrammatic representations of evolution have passed out of favor because the trunk of the tree failed to materialize, and I think it is clear that this failure was simply due to the fact that the trunk never existed. Although I suspect that this thesis could be successfully argued for any major group I will confine myself to plants with which I have some special interest and which bear on the problem of *Crocalophyton*.

It is becoming apparent, even in non-paleobotanical circles, that the term "psilophyte" cannot be defined with any degree of precision. From the seemingly simple (one might say classical) example of *Rhynia* a considerable diversity of morphology is now known; this has been dealt with briefly but effectively by Miss Leclercq (1954). The complexity in stelar anatomy that exists in Devonian and lowermost Mississippian plants is perhaps not so well known. I refer particularly to the stelar pattern in *Rhynia*, *Asteroxylon* and the assemblage of more complicated forms including *Pietzschia*, *Steloxylon*, *Siderella*, *Cladoxylon*, *Xenocladia*, and *Periastron*.

The problem of relationships among certain of these Devonian and Mississippian fossils is a perplexing one, but, since in some stems only anatomy is known while in others our information is more or less limited to the gross morphology, any postulated relationships are obviously tentative. It is, however, instructive to contrast the stelar anatomy of plants of the *Rhynia* type with the more complex polystelic fossils such as *Steloxylon* and *Xenocladia*. The fragment of the stem of *Xenocladia* described by Arnold (1952a) from the Middle Devonian of New York measures approximately 1×5 cm. in cross-section (suggesting a stem of about 10 cm. diameter) and includes more than 40 steles. Several fragmentary specimens of *Steloxylon* have been collected from the New Albany shale, the largest of which are about 3×6 cm. and are composed of several dozens of steles. The contrast between plants of this sort and those possessing slender monostelic stems presents a deep and broad chasm to be spanned by any evolutionary bridge. It is possible that they may have originated from an earlier, indeed much earlier, common land plant ancestor but since there is no evidence to support this it seems at least equally reasonable to postulate separate ancestry prior to establishment of the land habit.

Taking size and form relationships into consideration, if an early land plant were *originally* large we might expect to find *either* a large stelar unit *or* several centers of stelar organization.

Prototaxites is an example of an early (possibly land) plant with longitudinally aligned conducting cells throughout the trunk. This does not in any way imply a brown algal ancestry for the groups that were successful in accommodating themselves to the land habitat, but I believe it does present potentialities for a conducting system wholly different from the *Rhynia* type.

Crocalophyton affords evidence that a plant of large diameter (as compared with the *Rhynia* type) did exist and it apparently possessed an extensive apical

meristem of a somewhat indecisive character. Conducting cells that are "almost tracheids" were formed but in a very irregular fashion and apparently not constantly, as is evinced by the vertical stratification of "vascular" and non-vascular tissues. Briefly, it may be concluded that *Crocalophyton* is an early land plant wholly different from the classical *Rhynia*.

We are accustomed to look upon *Rhynia* as "typical" or as a central type of the psilophytes; at least it seems to occupy this position in most general accounts and texts. I believe it occupies this position chiefly because of the excellence and completeness of the preservation. What we do know to be a fact is that the early vascular plants were, by Devonian times and probably earlier, a highly complex assemblage. It would seem to follow that these plants were highly polyphyletic; they were radiating out in many directions a few of which became definable as lycopods, articulates, coenopterids, etc. There can be no doubt that we have only a fragmentary picture of this polyphyletic plan; discoveries of the future may or may not clarify the path followed by the more successful groups of the Carboniferous but they will certainly add to the complexity of the polyphyleticism that is already evident.

It seems clear that once a distinctive pattern of organization is established it may radiate in many directions, and there may or may not be a conspicuous channel which leads to another basic pattern. It is evident that the articulates and ferns (and I should think to a somewhat lesser degree the lycopods) diversified rapidly in many directions, although it would seem to be more difficult to define what we mean by a fern than an articulate because of a greater polyphyleticism in the former group.

The degree of morphological diversity that has existed in the algae is enormous, and it is very likely that they were highly diversified in pre-Cambrian times. The point, therefore, that I have attempted to lead to is that in all probability several (or many) groups of algae participated in the attempt to conquer the land. May we possibly explain the diversification of morphology and anatomy that exists in the early lycopods, articulates, the "psilophytes", as well as the many that "do not fit" as representing numerous lines of evolution from the algae rather than just three or four? I believe this viewpoint receives support from other "groups" or plants that defy classification. I allude here to fossils such as *Protosalvinia* and *Prototaxites*.

Arnold (1954) notes:

The position of *Protosalvinia furcata* in the plant kingdom is unknown, but it had evolved to a level ^[6] comparable to that of the lower bryophytes. . . . Not being connected with vascular plant evolution, the rise of *Protosalvinia* during Devonian time was a minor episode of nature, one of many attempts to preserve and perpetuate life by meeting adversity through adaptation and adjustment. This attempt was apparently not more than temporarily successful and was inadequate to insure continuity of the particular line. As far as we know *Protosalvinia* gave rise to no other forms and has no descendants. [p. 299].

⁶ I have underlined the word *level*. There is a subtle distinction between classing a plant as a member of the *Bryophyta* and saying that it has reached that level.

With reference to *Prototaxites*, the relations of this curious plant have recently been reviewed by Arnold (1952b) in a contribution which includes a description of a beautifully preserved new species. Not only is the taxonomic position of *Prototaxites* very much in doubt but its habitat is as well; suggestions of various authors place it anywhere from the deep sea to a land habitat.

As to *Crocalophyton* I can only conclude that it represents a curious effort, one of a great many, in the struggle to evolve a vascular flora. Very possibly it or its immediate descendants reached a dead end; at any rate it has no known contemporaries with which it may be closely compared.

Acknowledgement:—

Because of the exceptional problems involved in the matters of anatomical interpretation and the establishment of natural affinities we have called upon authorities in several fields for advice. Their suggestions have been most helpful and of not a little comfort although the authors assume responsibility for the tentative conclusions that have been reached. We are particularly indebted to: James M. Schopf, Charles J. Felix, Gilbert M. Smith, G. F. Papenfuss, and Johannes Proskauer. Special thanks are due Sergius H. Mamay for kindly placing the specimens in our hands for study and for assistance during the course of the investigation.

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EXPLANATION OF PLATE

PLATE 4

Crocalophyton readi Andrews and Alt

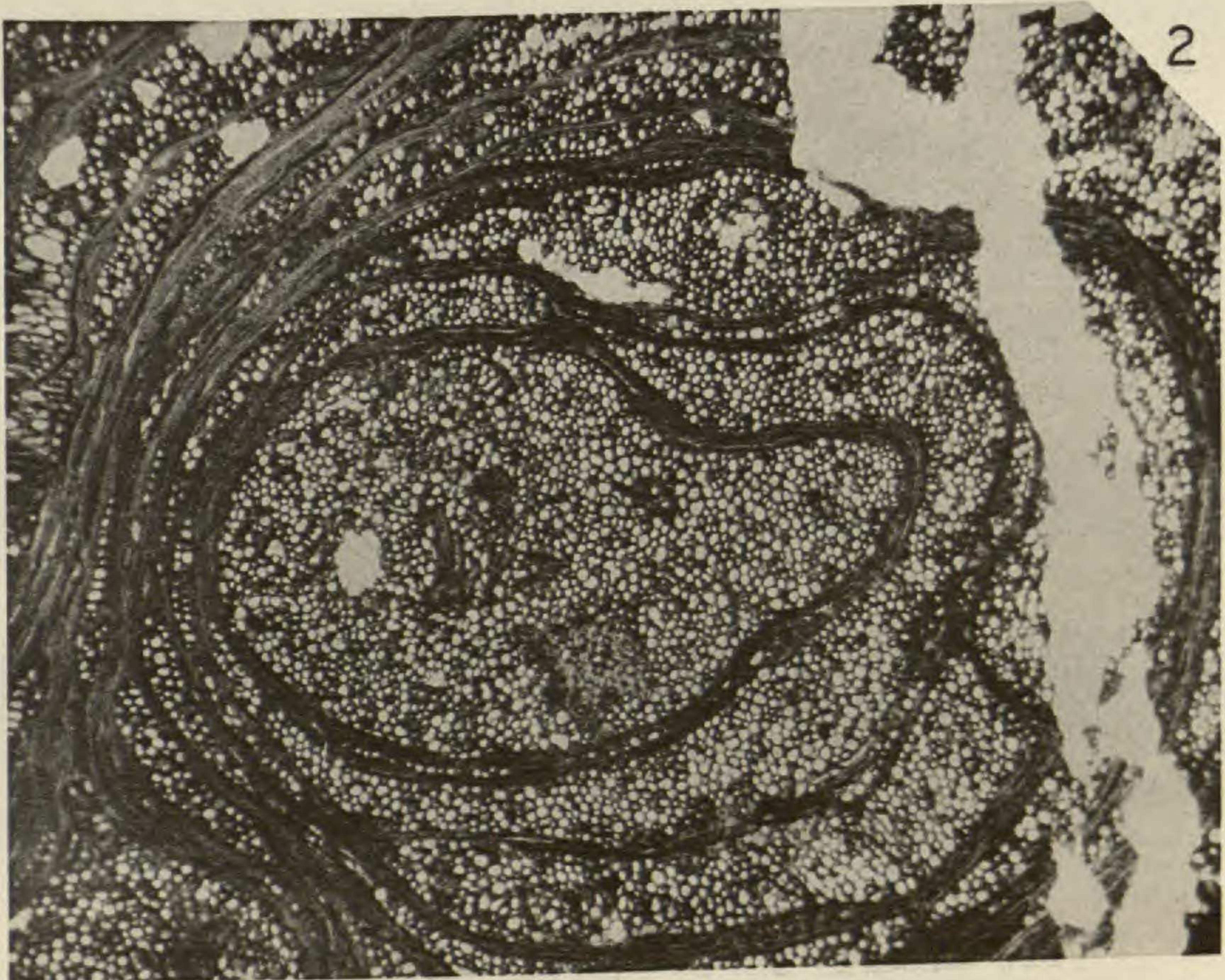
Fig. 1. Specimen No. 40798 (U.S.N.M.), approximately natural size.

Fig. 2. Detail of transverse section showing looped form of strands. 23X. Slide B1C,b1.

NOTE: All figured slides are preserved in the Paleobotanical collections of the United States National Museum. Slide numbers noted herein indicate the position from which they were prepared as indicated in text-fig. 1.

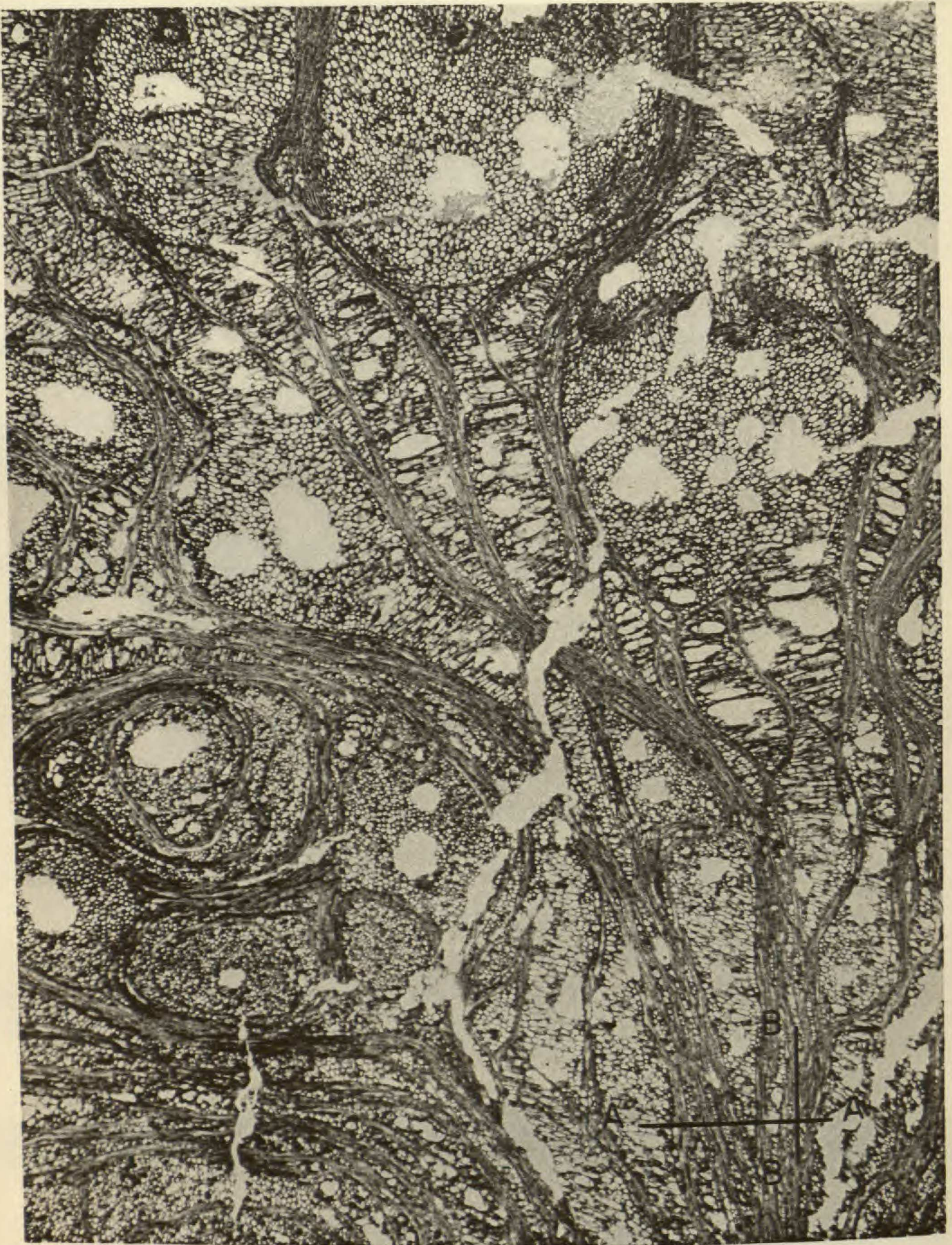


1



2

ANDREWS AND ALT — *CROCALOPHYTON READI*



3

EXPLANATION OF PLATE

PLATE 5

Crocalophyton readi Andrews and Alt

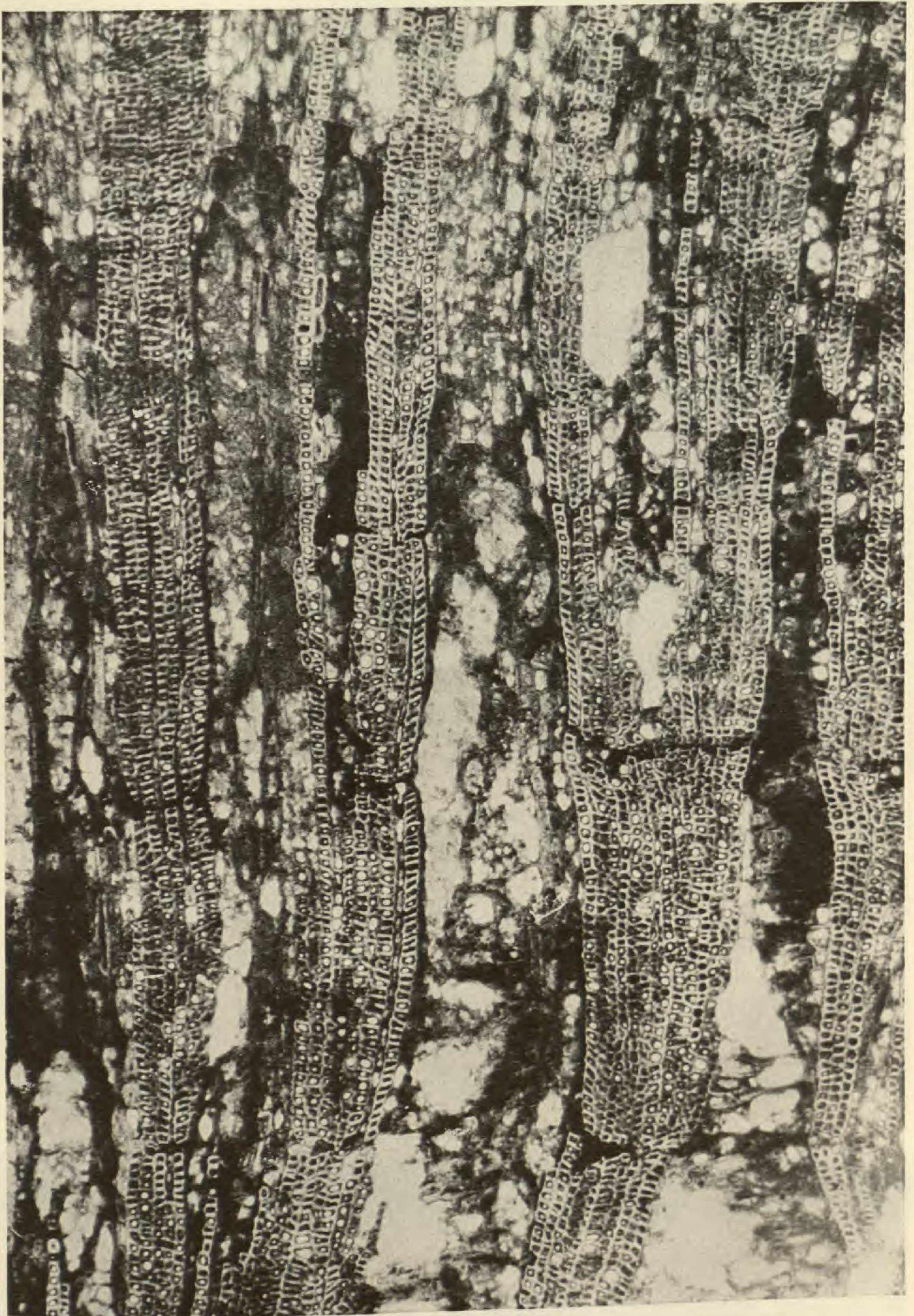
Fig. 3. Transverse view through a representative portion of a strand zone. Line A-A indicates orientation of "tangential" section (see fig. 4); line B-B indicates orientation of "radial" section (see fig. 5). 14X. Slide B1C,b1.

EXPLANATION OF PLATE

PLATE 6

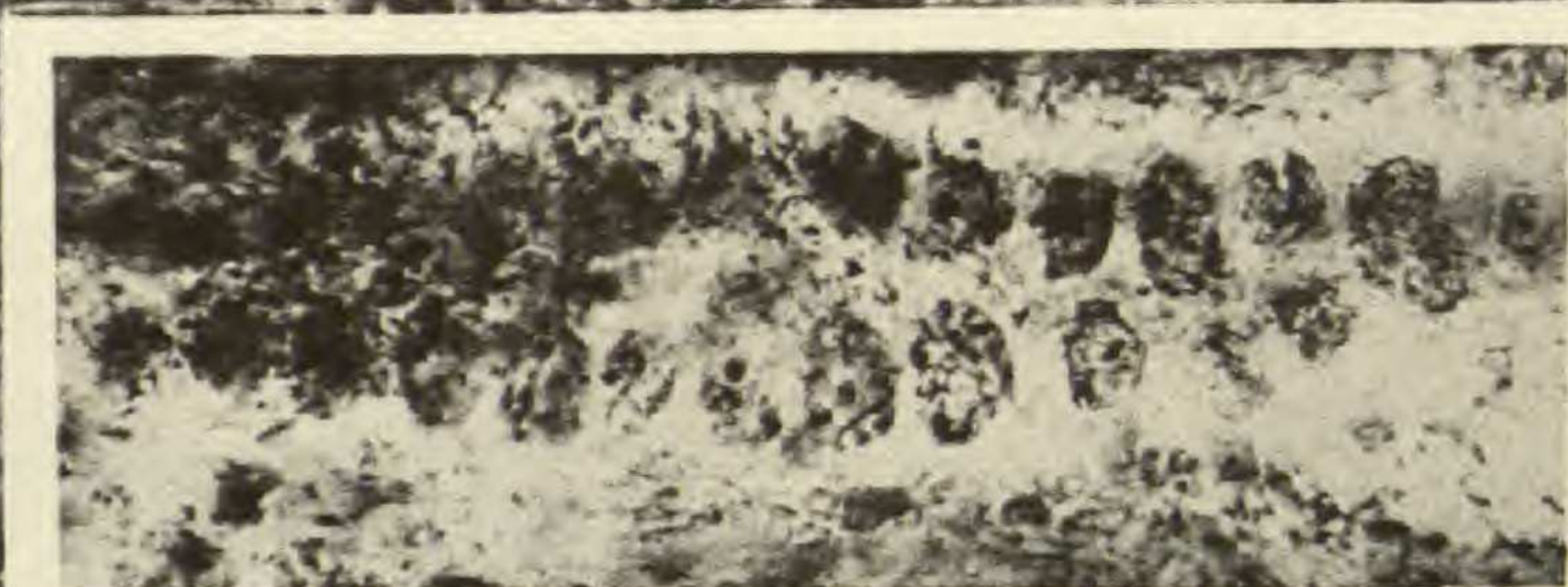
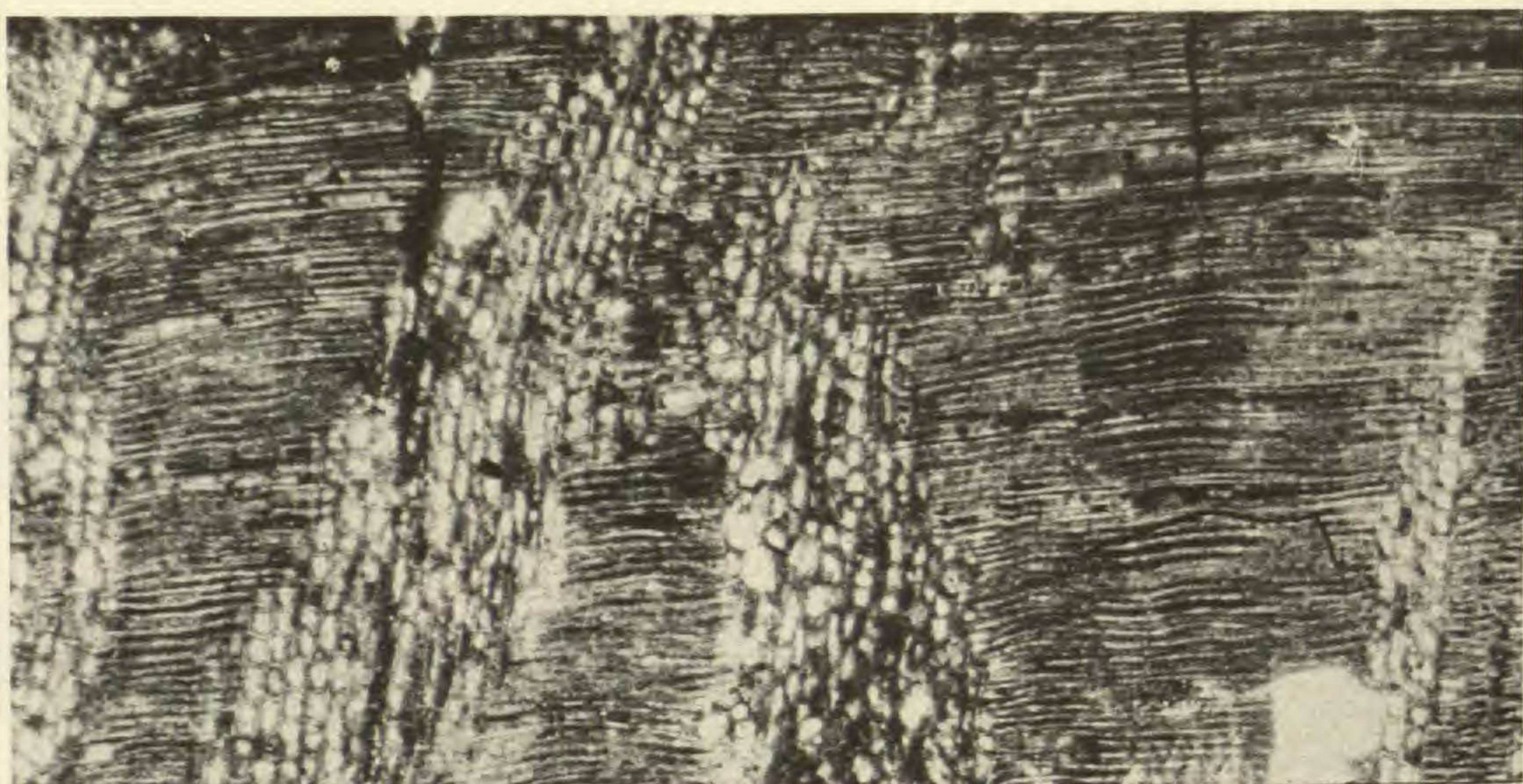
Crocalophyton readi Andrews and Alt

Fig. 4. Strands in tangential view. 40X. Slide A2-2, s2.

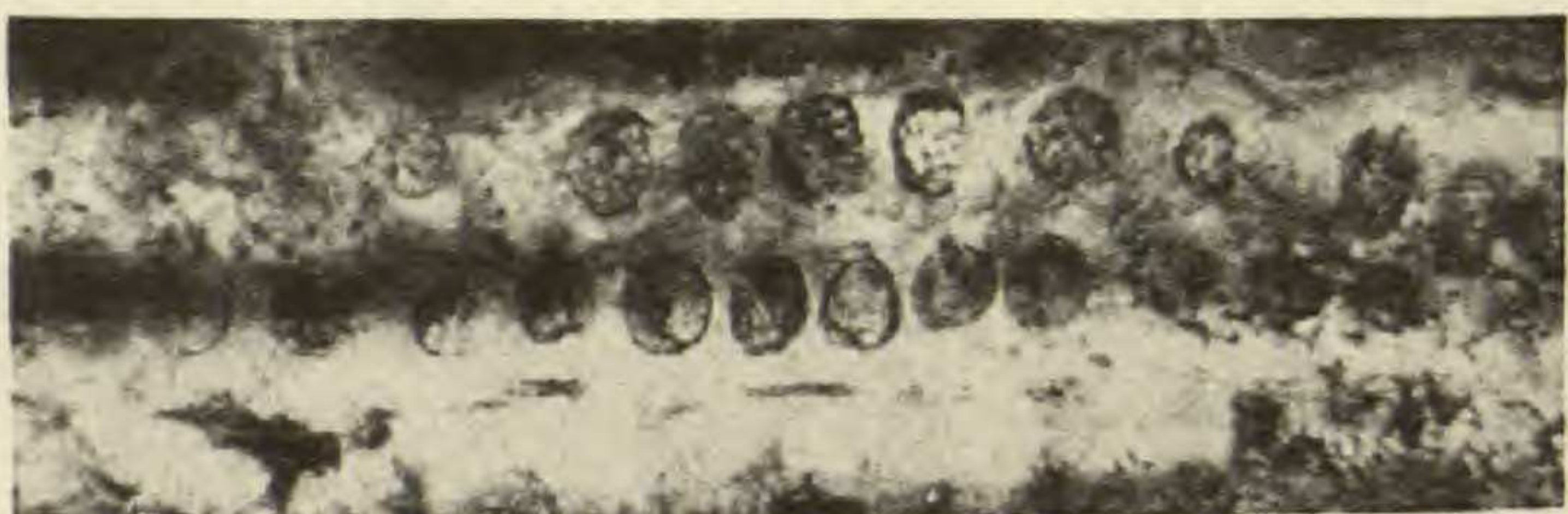


4

ANDREWS AND ALT — *CROCALOPHYTON READI*

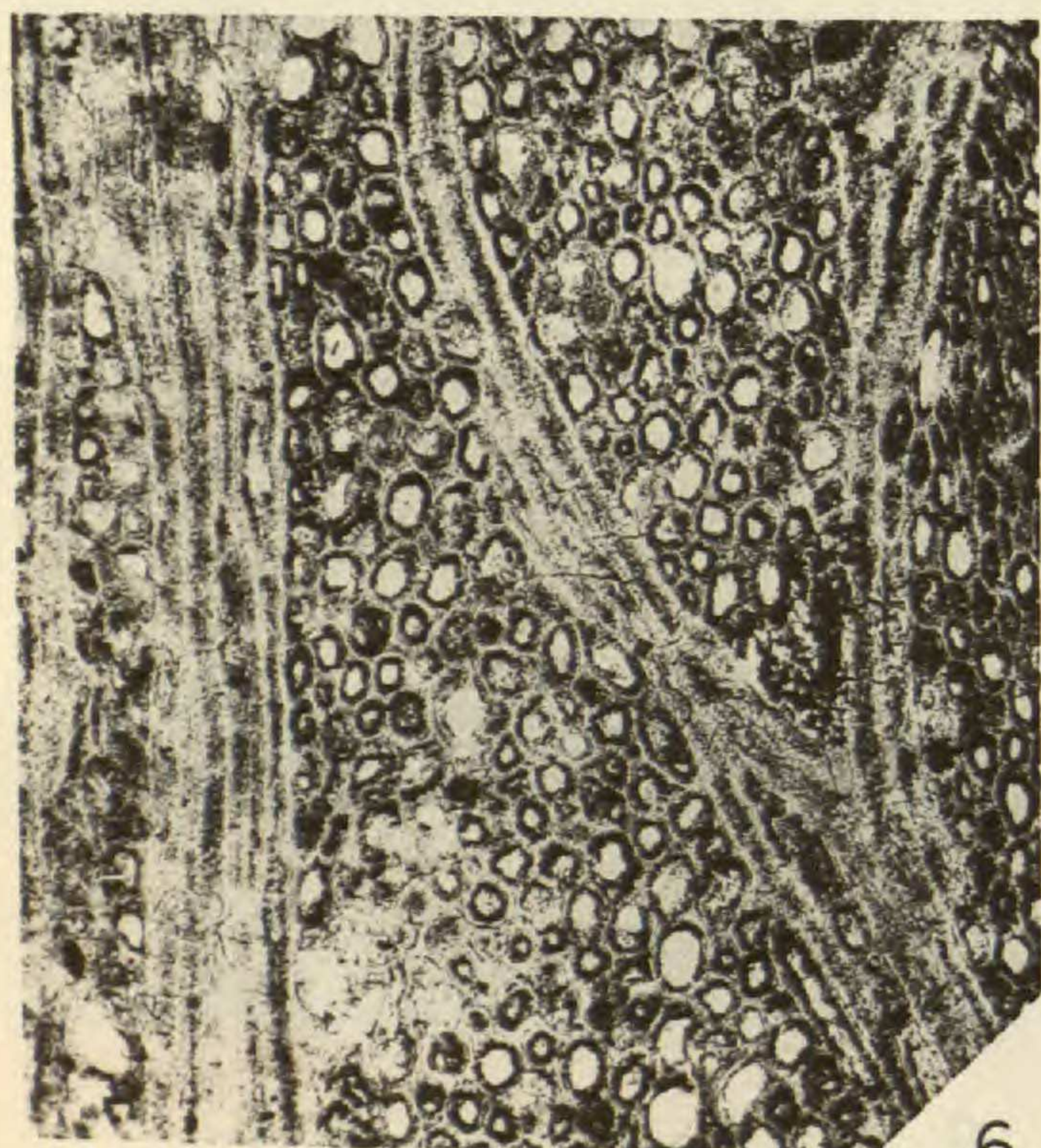


5A

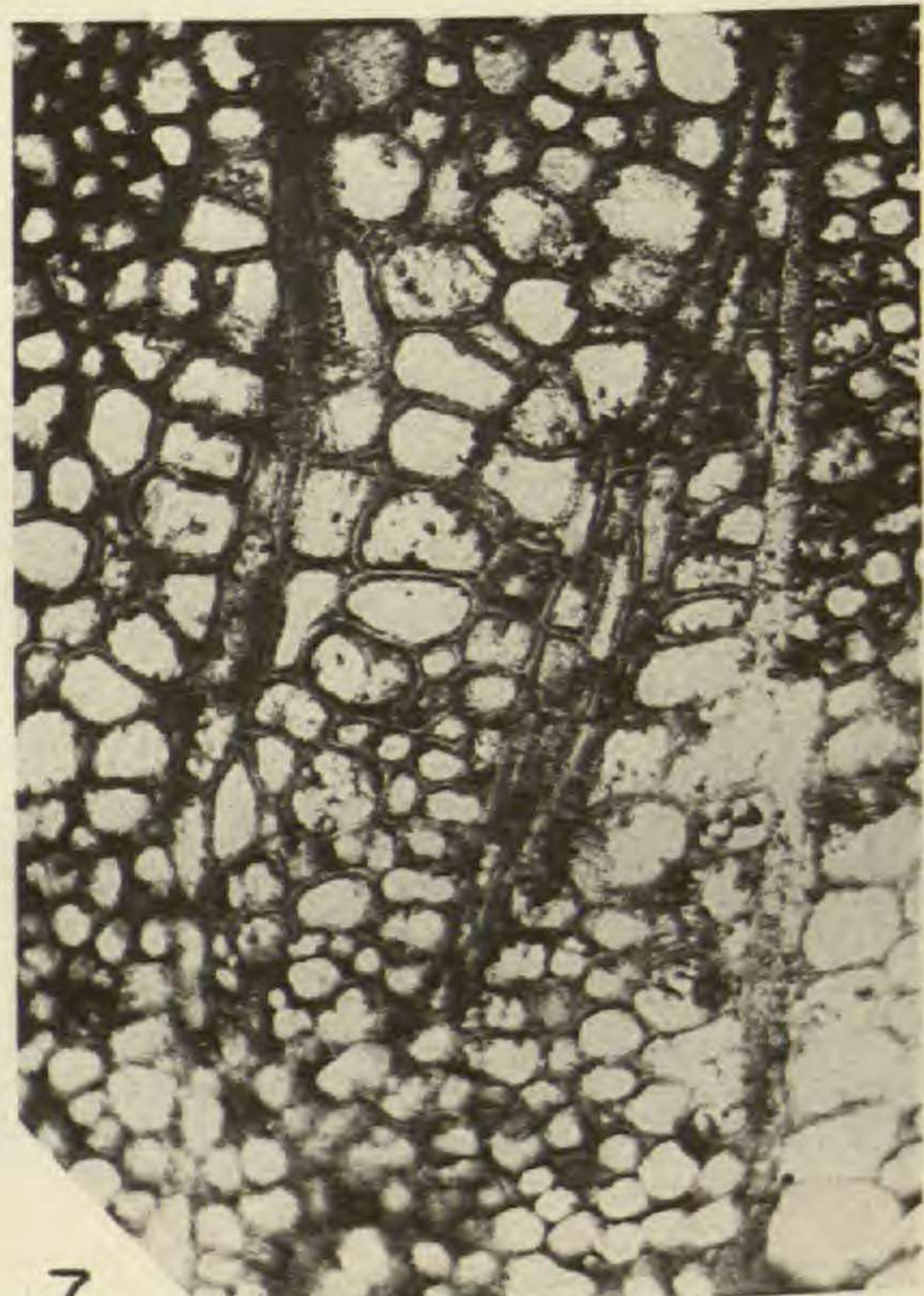


5B

5



6



7